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Persistence and Yield Stability of Intersubspecific Alfalfa Hybrids

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ABSTRACT

Long-term persistence and sustained biomass yields of alfalfa (*Medicago sativa* L.) stands are important to producers. Yield performance and persistence of intrasubspecific crosses between alfalfa subspecies *sativa* and *falcata* after the first post-establishment year are unknown. The objectives of this study were to measure biomass yields, persistence, and biomass yield stability in inter- and intrasubspecific alfalfa crosses derived by mating nine elite sativa clones and five falcata clones in a half-diallel. Progeny were space planted in 1998 at Ames and Nashua, IA, and evaluated for persistence, biomass yield, and biomass yield stability from 1998 through 2002. *Medicago sativa* subsp. *sativa* (sativa) × *M. sativa* subsp. *falcata* (falcata) hybrids produced substantial biomass yield and exhibited heterosis through the first post-establishment year, but declined in subsequent years. From 1998 through 2002 the intersubspecific hybrids had persistence equivalent to the more persistent parental subspecies, with the effect becoming more apparent as time progressed. Intrasubspecific hybrids had less biomass yield stability than the more stable intrasubspecific sativa crosses. The results indicate that selection of improved falcata germplasm for long term persistence and higher yield is needed.

Breeding methods to capitalize on heterosis, such as semihybrids (Brummer, 1999) or hybrids using a male sterility system (Wagner et al., 2003), have been developed but are not widely used in the alfalfa industry. We have reported previously that *M. sativa* subsp. *sativa* (hereafter sativa) and *M. sativa* subsp. *falcata* (hereafter falcata) represent heterotic breeding pools for biomass yield (Westgate, 1910; Waldron, 1920; Sriwatanapongse and Wilsie, 1968; Riday and Brummer, 2002a, 2005). We have also investigated the heterotic effects of sativa × falcata alfalfa hybrids for nutritive value and agronomic traits (Riday et al., 2002; Riday and Brummer, 2002b, 2004). However, both our results and those of the other experiments were based on data obtained in the establishment and first production years, when little time had elapsed for the cumulative effects of stress to impact stand persistence.

Long-term stand persistence is important for the economical production of alfalfa because it allows the costs of seeding to be amortized over a longer period. Persistence is a complex trait affected by a large number of factors, including grazing, mechanical harvesting equipment, intensity of harvest management, diseases and pests, cold weather, inadequate dormancy, and inter- and intraspecies plant competition. Numerous breeding programs have used artificial and natural selection to develop improved alfalfa germplasm able to withstand various plant stresses, thereby increasing stand life (Brummer and Moore, 2000; Kallenbach et al., 2002). Most breeders agree that to truly select for persistent alfalfa requires long-term evaluation of plants and selection among survivors in advanced stand years (Gallepp, 1997). Commercial alfalfa breeding programs typically select plants after 3 to 5 yr in the field.

In addition to yield per se throughout the life of the stand, consistently superior performance over environments is also desirable. Cultivar stability can be assessed by testing germplasm in many different environments and selecting genotypes that perform well in most environments (Fehr, 1991). Studies have shown that increased heterozygosity of individual plants and increased heterogeneity of plant mixtures often lead to increased environmental stability (Allard and Bradshaw, 1964). These findings led us to suspect that sativa × falcata hybrids should be more stable than intrasubspecific synthetics.

The purpose of this study was to examine biomass yield, plant persistence, and biomass yield stability in intersubspecific hybrids of sativa and falcata over the 5 yr of the stand. The first objective was to determine biomass yields in advanced years of production and to determine if the hybrid yield advantage identified in the establishment and first production years (Riday and Brummer, 2002a) held in subsequent production years as the stand aged. Our second objective was to determine if sativa × falcata hybrids had superior persistence. Our final objective was to determine if intersubspecific hybrids had more stable yields than intrasubspecific crosses in Iowa environments.

MATERIALS AND METHODS

Plant Material

Nine sativa and five falcata genotypes were crossed in a half-diallel mating design as previously described, with sativa serving as females in hybrid crosses (Riday and Brummer, 2002a). The nine elite sativa genotypes included ABI408, ABI311, ABI419, ABI314, C96–514, C96–673, C96–513, FW-92–118, and RP-93–377; the five falcata genotypes included WISFAL-4, WISFAL-6, C25–6, PI214218–1, and PI502453–1. Progeny were germinated in March 1998 in the greenhouse and stem cuttings of parental genotypes were made at this

Abbreviations: falcata, *Medicago sativa* subsp. *falcata*; FFC, falcata × falcata crosses; GCA, general combining ability; HS-heterosis, heterosis on a half-sib basis; HSHP, parent heterosis on a half-sib basis; sativa, *Medicago sativa* subsp. *sativa*; SCA, specific combining ability; SFHS, sativa × falcata half-sib; SFC, sativa × falcata crosses; SSC, sativa × sativa crosses; WHS, within-subspecies half-sib.

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time. A total of 110 entries was included in this experiment (91 crosses; 14 parental clones; and 5 check varieties [Vernal, 5454, Innovator +Z, Ladak, and Legendairy]). More detail on greenhouse work is given in Riday and Brummer (2002a).

Field Design

Field experiments were planted at the Agronomy and Agricultural Engineering Research Farm west of Ames, IA, in a Nicollet loam soil (fine-loamy, mixed, superactive, mesic Aquic Hapludoll) on 20 May 1998 and at the Northeast Research Farm south of Nashua, IA, in a Readlyn loam (fine-loamy, mixed, superactive, mesic Aquic Hapludoll) on 22 May 1998. The plot design at Ames was a quadruple α-lattice, with 10 plots in each of 14 incomplete blocks for 560 total plots. At Nashua the design was a quadruple α-lattice, with nine plots in each of 14 incomplete blocks for a total of 504 total plots. Ten plants per plot were planted 30 cm apart within rows spaced 90 cm apart. Entries were separated by 60 cm within rows. Biomass yield on a dry matter basis was measured during 3 yr postestablishment, with three harvests per year (Ames: 18 Aug. and 16 Oct. 1998; 27 May, 7 July, and 1 Sept. 1999; 26 May, 17 July, and 1 Sept. 2000; 13 June, 30 July, and 14 Sept. 2001; and 22 May, 1 July, 18 Aug. 2002. Nashua: 20 Aug. and 20 Oct. 1998; 6 June, 15 July, 10 Sept. 1999; 31 May, 20 July, and 7 Sept. 2000; 14 June, 23 July, and 11 Sept. 2001; and 14 June, 18 July, and 13 Sept. 2002). Based on plant counts in each plot, biomass yield was calculated on a gram per plant basis.

Plant counts for persistence were taken before the August 1998 harvest, which was the initial plant count. In the autumn of 1999 to 2002 plant counts were taken on each plot and a percentage of plants surviving based on the initial count was calculated.

Data Analysis

Statistical analyses were conducted on total yearly dry matter yield and persistence percentages. Replication and blocks were considered random effects. The MIXED procedure of the SAS statistical software package (SAS Institute, 2000) was used to calculate least squared means for each entry in each location-year combination.

To compare the different types of crosses for biomass yield and persistence during each year, the 91 crosses from the 14 parent half-diallel were divided into three categories: (i) sativa × sativa crosses (SSC), (ii) sativa × falcata crosses (SFC), or (iii) falcata × falcata crosses (FFC). Comparisons among the three groups were calculated using linear contrasts (SAS Institute, 2000). A mid-subspecies mean was calculated as the average of the SSC and the FFC means. The mid-subspecies mean was compared with the SFC mean using a linear contrast (SAS Institute, 2000). If the comparison between them was significant, a deviation percentage was calculated, which represents average heterosis or mid-subspecies heterosis. Comparisons of entry and stability variances (entry by location, by year, by location × year, and by environment [treating location–year combination as environments]) for yield among cross types (SSC, SFC, and FFC) was done using an equality of variance test (Snedecor and Cochran, 1967).

General (GCA) and specific combining ability (SCA) were calculated using SAS (Zhang and Kang, 1997). The analysis used Model I Method 4 from Griffing (1956) which includes F_1 progeny, but not reciprocal crosses or parents and in which genotypes are fixed. The mean half-sib family performance of each parental genotype for biomass yield and persistence was calculated for both inter- and intrasubspecies crosses. The two half-sib means, sativa × falcata half-sib mean (SFHS) and within-subspecies half-sib mean (WHS), for each genotype were contrasted (SAS Institute, 2000). High parent heterosis on a half-sib basis (HSHP) was calculated using linear contrasts to compare the sativa × falcata half-sib mean of a given parental genotype with the larger of the following: (i) the parental genotype's within-subspecies half-sib mean or (ii) the within subspecies cross mean (SSC or FFC) of the subspecies in which the parental genotype was not found (SAS Institute, 2000). Mean heterosis on a half-sib basis (HS-heterosis) was calculated by comparing each parental genotype's sativa × falcata half-sib mean performance to the average performance of intrasubspecies crosses (2002a).

RESULTS AND DISCUSSION

Multiyear Forage Yield

Experiment wide mean biomass yield showed SFC inferior to SSC but superior to FFC, with mid-subspecies heterosis at 9% (Table 1). During 1998 and 1999, SFC were superior to SSC, which were superior to FFC, as reported previously (Riday and Brummer, 2002a). Mid-subspecies heterosis was highest in 1999, at 18% (Table 1). In 2000 SFC and SSC were equivalent and superior to the FFC with mid-subspecies heterosis at 11%. In 2001 and 2002, the third and fourth post-establishment years, SFC fell between the two intrasubspecific crosses, with mid-subspecies heterosis declining to 8 and 1%, respectively (Table 1). Combining ability analysis revealed significant general combining ability (GCA) and specific combining ability (SCA) effects during each year except the last year (2002) when no SCA was measured (Table 1). Previously we reported that the SFC showed a greater tendency toward positive SCA compared with the intrasubspecific crosses (Riday and Brummer, 2002a).

A more in-depth analysis on a location basis revealed increasing annual yields from the establishment year (1998) at Ames through 2000 after which yields declined (Fig. 1). The northern location, Nashua, had lower yields than Ames for 4 of the 5 yr, consistent with previous experiments and statewide variety trials (Brummer and Smith, 2000; Riday and Brummer, 2002a, 2004). The

Table 1. Mean alfalfa dry matter yield (g plant^{-1}) for crosses between and within *M. sativa* subsp. *sativa* (sativa) and *M. sativa* subsp. *falcata* (falcata), mid-subspecies heterosis (MS-heterosis), and general and specific combining ability (GCA and SCA) at two Iowa locations during the establishment year and first through fourth post-establishment years (1998–2002).

Cross type	No. crosses	Mean yield	Year 1998	1999	2000	2001	2002
		g plant^{-1}					
sativa × sativa	36	235a†	51b	149b	346a	306a	325a
sativa × falcata	45	228b	55a	164a	336a	285b	300b
falcata × falcata	10	184c	46c	128c	258b	221c	268c
MS-heterosis		9%***	15%***	18%***	11%***	8%***	1%‡
GCA		***	***	***	***	***	***
SCA		***	*	**	*	**	NS

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Yields within columns followed by different letters are significantly different at $P = 0.05$.
‡ NS, not significant.

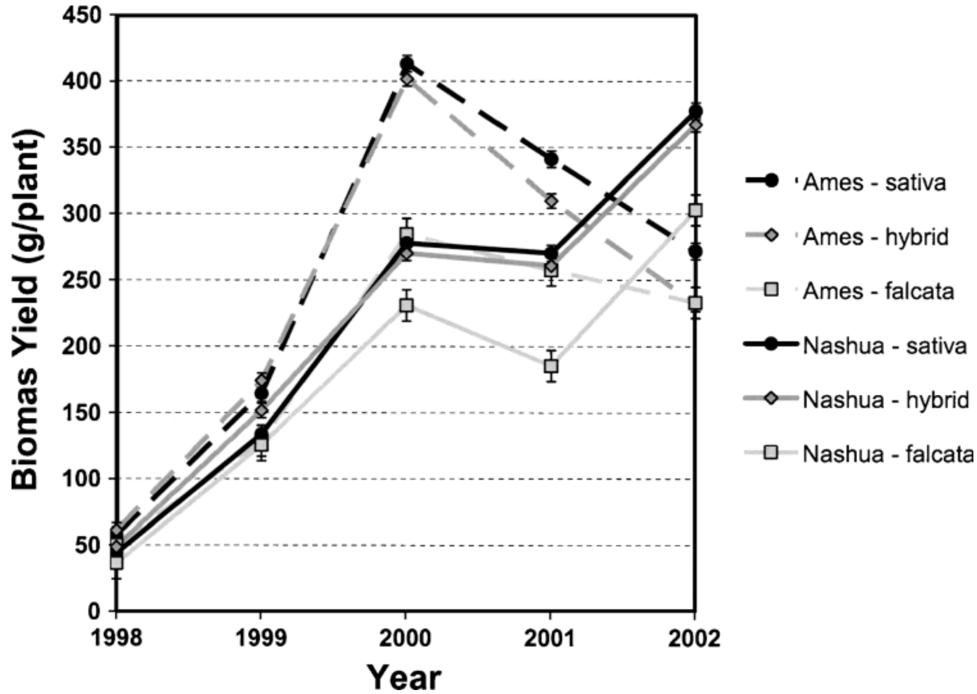

Fig. 1. ***Medicago sativa*** **subsp.** ***sativa*** **(sativa),** ***M. sativa*** **subsp.** ***falcata*** **(falcata), and sativa × falcata hybrid dry matter yield (plant^{-1}) from 1998 to 2002 at two Iowa locations (Ames and Nashua).**

declining mid-subspecies heterosis from 2000 to 2002 observed on the experiment wide basis can be explained by location effects. In Nashua the SFC and SSC produced similarly throughout the life of the stand, with FFC performance lower than either during second through fourth post-establishment years (Fig. 1). In Ames SFC and SSC produced similar yields through the second post-establishment year. However, during 2001 and 2002, the SFC declined in relation to SSC, becoming closer to the FFC performance levels (Fig. 1). Ames was likely a more demanding environment for the experiment, with hotter midsummer temperatures and heavier, poorly drained soils. The observed third and fourth post-establishment year yield declines in SFC could result from increased disease pressure in Ames, which would be more severe on germplasm containing the less improved falcata parentage.

Individual genotypes had varying sativa × falcata hybrid performance levels (Table 2). On an experiment wide basis, all sativa genotypes exhibited within subspecies half-sib means (WHS) that were equivalent to their sativa–falcata half-sib (SFHS) counterparts except genotypes ABI311, ABI314, and ABI419 (Table 2). All falcata genotypes had SFHS means superior to those of WHS on an experiment wide basis. In 1998 five out of fourteen genotypes showed high-parent half-sib heterosis (HPHS) in sativa × falcata hybrids. All falcata genotypes produced SFHS superior to WHS and both progeny types were equivalent for most sativa genotypes (Table 2). During 1999 SFHS were superior to WHS for all sativa genotypes except the four ABI genotypes. Of the ten genotypes with superior SFHS, all showed HPHS except C25–6 (Table 2). In contrast, by the second post-establishment year (2000), most of the sativa genotypes showed no differences between SFHS and WHS; two ABI genotypes even show inferior SFHS values. All falcata genotypes, except C25–6 still produced SFHS progeny superior to WHS progeny, and WISFAL-4 showed HPHS. The same trend was observed in the third post-establishment years. By the fourth production year, virtually no differences were observed between progeny types (Table 2).

Individual genotypes, for the most part, followed mid-subspecies heterosis averages, with maximum heterosis observed during the first post-establishment year and declining in subsequent years (Table 2, Fig. 1). The ABI genotypes, except ABI 408, showed positive HS-heterosis in 1999, after which values drop and become negative by the fourth post-establishment year (Table 3). The Forage Genetics genotypes C96–513 and C96–514 showed positive HS-heterosis throughout the experiment, with only modest declines in 2002. Genotypes ABI408, C96–673, FW-92–118, RP-93–377, WISFAL-4, and WISFAL-6 exhibited HS-heterosis in 1999, but these values declined across subsequent years in all cases, reaching non-significance by 2002 (Table 2). Finally, genotypes PI214218–1 and PI502453–1 show strong HS-heterosis in 1999, but not in any subsequent years.

Hybrid performance was much more similar to that of SSC than FFC over locations and years with exception of Ames 2002 location (Fig. 1). This is strong evidence that the basis of sativa–falcata heterosis is due to partial to complete dominance (Hallauer and Miranda, 1988; Woodfield and Bingham, 1995) of the superior parental subspecies (SSC) compensating for the poorer parental subspecies (FFC), resulting in hybrids with good performance. We made a similar observation for stem cellulose and hemicellulose levels in FFC, SFC, and SSC,

Table 2. Inter- and intrasubspecific half-sib (SFHS and WHS, respectively) family dry matter yield (g plant^{-1}) means for 14 alfalfa genotypes measured during establishment and first through fourth post-establishment years (1998–2002) at two Iowa locations.

	Experiment mean		1998		1999		2000		2001		2002	
Genotype	SFHS	WHS†	SFHS	WHS	SFHS	WHS	SFHS	WHS	SFHS	WHS	SFHS	WHS
	g plant^{-1}											
ABI311	188	219***	55‡	56**	154	155	254	309**	216	279***	251	297*
ABI314	202	220*	51	53	162	149	295	325	243	278**	257	294
ABI408	248	256	62‡	55*	167	162	378	384	311	332	324	347
ABI419	178	202**	43	45	140	137	249	290*	213	262***	244	274
C96–513	277	264	61	49***	169‡	148**	418	392	361	351	376	381
C96–514	259	249	52	49	162‡	143*	392	374	342	332	345	348
C96–673	223	222	50	46	167‡	139***	329	327	278	292	289	304
FW-92–118	242	238	52	50	176‡	154**	375	351	292	298	313	336
RP-93–377	235	247	59	54	172‡	155*	333	359	313	325	298	344*
WISFAL-4	244	189***	57‡	45***	166‡	128***	387‡	284***	291	237***	317	253**
WISFAL-6	245	190***	52	42***	170‡	133***	358	279***	319	222***	326	274*
C25–6	235	206***	53	44**	144	122**	335	301	306	245***	335	316
PI214218–1	204	164***	56‡	47***	159‡	129***	291	203***	255	200***	257	241
PI502453–1	212	169***	57‡	39***	176‡	124***	309	221***	255	203***	263	257
Sativa mean		235		51		149		346		306		325
Falcata mean		184		43		127		258		221		268
LSD(0.05)		14		6		14		36		24		44

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Within subspecies halfsib means (WHS) were contrasted with sativa × falcata halfsib means (SFHS).
‡ SFHS value exhibited high parent halfsib heterosis (HSHP-heterosis).

and termed this phenomenon "subspecies dominance" (Riday et al., 2002). Subspecies dominance does not preclude the possibility that the weaker subspecies has useful alleles. In tomato (*Lycopersicum esculentum* Mill.) useful quantitative trait loci (QTL) were identified in exotic tomato germplasm that enhanced elite germplasm performance (Gur and Zamir, 2004). In this study, the superiority of SSC over FFC may mask useful biomass yield alleles within the falcata germplasm. In this study, all genotypes did not perform equally in sativa × falcata crosses; three of the ABI genotypes and C25–6 were particularly inferior. Riday and Brummer (2005) demonstrated that falcata germplasm with a European origin showed greater biomass yields and yield heterosis than Asian material. By increasing favorable gene-frequencies in falcata breeding populations, these populations should perform more similar to elite sativa populations, which may result in more complimentary gene action (Bingham et al., 1994), whereby favorable dominant alleles in each population lead to progeny expressing high parent heterosis.

Table 3. Dry matter yield halfsib heterosis (HS-heterosis) of 14 alfalfa genotypes grown across two Iowa locations during establishment and first through fourth post-establishment years (1998–2002).

Genotype	Experiment mean	1998	1999	2000	2001	2002
	HS-heterosis %					
ABI311	−7%*	30%***	9%	−10%	−14%**	−11%
ABI314	0%	6%	18%***	1%	−3%	−8%
ABI408	13%***	26%***	15%***	18%***	12%**	6%
ABI419	−8%*	−3%	6%	−9%	−12%**	−10%
C96–513	24%***	33%***	22%***	29%***	26%***	16%**
C96–514	20%***	12%*	20%***	24%***	24%***	12%
C96–673	10%**	13%*	25%***	12%*	8%*	1%
FW-92–118	15%***	12%*	25%***	23%***	13%**	4%
RP-93–377	9%**	21%***	22%***	8%	14%***	−3%
WISFAL-4	15%***	19%***	20%***	23%***	7%*	10%
WISFAL-6	15%***	12%*	20%***	15%***	21%***	9%
C25–6	6%**	13%**	6%	4%	11%**	5%
PI214218–1	2%	15%***	15%***	6%	1%	−9%
PI502453–1	5%	26%***	29%***	9%	0%	−9%

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.

In this study the female parents of the hybrids were always sativa genotypes. Our crossing design allows the possibility that hybrids performing similar to the superior subspecific parent is due to maternal effects of the sativa parent. This possibility seems less likely, however, since the sativa subspecies was not always the subspecies the hybrid was similar to across all traits measured (Riday and Brummer, 2002a, 2002b; Riday et al., 2002). The falcata subspecies had higher stem cellulose levels than the sativa subspecies with the hybrid for this trait being similar to the paternal falcata subspecific parent (Riday et al., 2002). If maternal effects were the basis of trait "subspecies dominance" we would expect to see the maternal species dominating for all such traits.

Persistence

After establishment in 1998, persistence was measured for the next 4 yr in the autumn of each year. No differences among cross types were observed in 1999 or 2000 (Table 4). During 2001 and 2002, the third and fourth year post-establishment, SSC and SFC were equivalent and had greater persistence than FFC. Initial persistence was lower in Nashua than in Ames (Fig. 2), possibly due to more severe winter conditions. In Ames, however, persistence declined more rapidly, reaching levels close to those seen in Nashua by the end of the experiment. At both locations, persistence of SSC and SFC remained similar throughout the experiment, indicative of subspecies dominance. However, the differences among cross groups were not sufficiently large

Table 4. Mean alfalfa persistence (%) for crosses between and within *M. sativa* subsp. *sativa* (sativa) and *M. sativa* subsp. *falcata* (falcata), mid-subspecies heterosis (MS-heterosis), and general and specific combining ability (GCA and SCA) at two Iowa locations for first through fourth post-establishment years (1999–2002).

Cross type	No. crosses	1999†	2000	2001	2002
		Persistence %			
sativa × sativa	36	91a	89a	87a	79a
sativa × falcata	45	91a	89a	86a	79a
falcata × falcata	10	92a	86a	80b	73b
MS-heterosis		−1%	2%	3%	4%
GCA		NS‡	NS	*	***
SCA		NS	NS	NS	***

* Significant at the 0.05 probability level.
*** Significant at the 0.001 probability level.
† Persistence within columns followed by different letters are significantly different at $P = 0.05$.

to produce mid-subspecies heterosis for persistence (Table 4). Significant GCA effects were not observed until 2001, the third post-establishment year, and SCA effects did not appear until 2002. Differences between WHS and SFHS persistence for any genotype were not observed until 2000 (Table 5) and occurred primarily in the falcata half-sib families.

Biomass Yield Stability

No differences among cross types were observed for entry variances (Table 6). Treating location–year combinations as environments, SFC had greater entry by environment variance than SSC, with FFC being similar to both. Subdividing entry by environment variance into three components (entry × location, entry × year, and entry × location × year) showed that SFC variances were greater than SSC variance for entry × location and entry × year (Table 6). Mid-subspecies heterosis was observed for entry × environment, entry × location, and entry × year variances (Table 6). The greater entry by environmental variances (i.e., greater instability) of

Table 5. Inter- and intrasubspecific halfsib (SFHS and WHS, respectively) family persistence (%) means for 14 alfalfa genotypes measured during first to fourth post-establishment years (1999–2002) across two Iowa locations.

Genotype	1999 SFHS	1999 WHS	2000 SFHS	2000 WHS†	2001 SFHS	2001 WHS	2002 SFHS	2002 WHS
	Persistence %							
ABI311	93	90	91	88	86	86	78	81
ABI314	89	93	88	90	87	87	80	74
ABI408	93	95	92	92	91	90	86	81
ABI419	88	91	87	90	86	89	80	82
C96–513	94	93	90	90	84	87	78	79
C96–514	87	90	86	87	83	84	76	79
C96–673	89	89	87	86	83	81	77	69*
FW-92–118	92	91	87	89	82	87	75	80
RP-93–377	96	91	94	90	89	88	78	83
WISFAL-4	94	96	92	95	88	92	82	88
WISFAL-6	88	94	87	89	85	84	78	76
C25–6	94	92	91	84	87	79*	79	71*
PI214218–1	90	89	89	85	86	78*	79	68**
PI502453–1	89	89	86	78*	82	70**	74	61***
Sativa Mean		91		89		87		79
Falcata Mean		92		86		80		73
LSD(0.05)		6		7		8		7

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Within subspecies halfsib means (WHS) were contrasted with sativa × falcata halfsib means (SFHS).

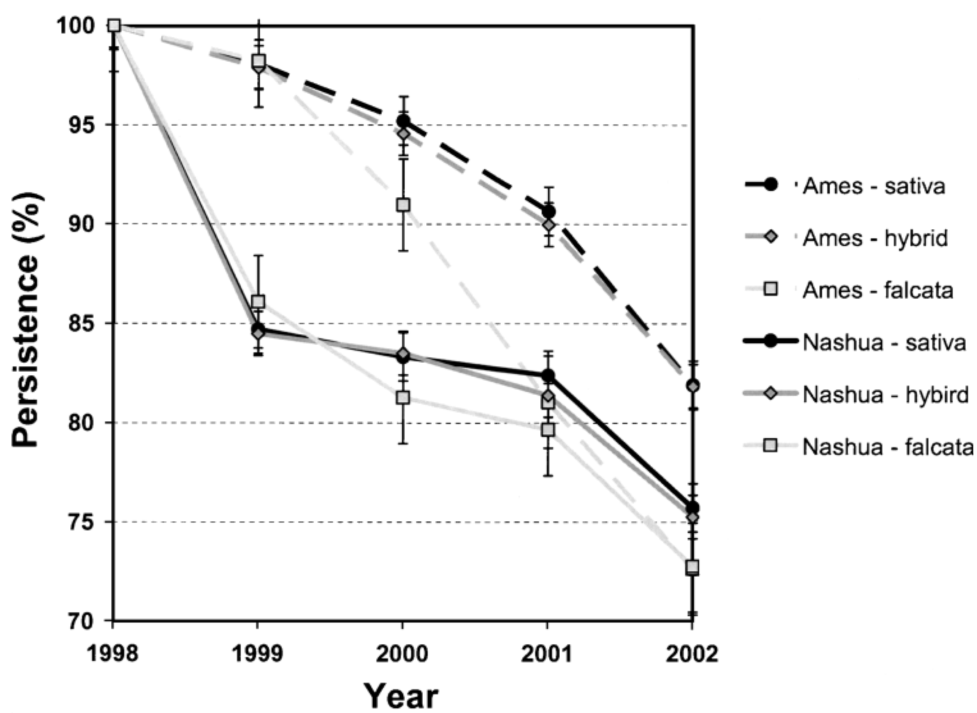

Fig. 2. ***Medicago sativa* subsp. *sativa* (sativa), *M. sativa* subsp. *falcata* (falcata), and sativa × falcata hybrid persistence (%) from 1998 to 2002 at two Iowa locations (Ames and Nashua).**

Table 6. Mean alfalfa biomass (g plant^{-1}) entry (i = 1. 91), entry × environment (iE), entry × location (iL), entry × year (iY), and entry × location × year (iLY) variances for crosses between and within *M. sativa* subsp. *sativa* (sativa) and *M. sativa* subsp. *falcata* (falcata) with variance mid-subspecies heterosis (MS-heterosis), and general combining ability (GCA) at two Iowa locations during 5 yr.

Cross type	No. crosses	Entry interaction				
		σ^2_i	σ^2_{iE}	σ^2_{iL}	σ^2_{iY}	σ^2_{iLY}
		g plant^{-1}				
sativa × sativa	(36)	893a†	1327a	24a	360a	994a
sativa × falcata	(45)	1136a	1946b	134b	914c	1059a
falcata × falcata	(10)	580a	1665ab	75b	550b	1134a
MS-heterosis		54%‡	30%*	172%*	101%***	−1%‡
GCA		–	***	NS	NS	*

* Significant at the 0.05 probability level.
*** Significant at the 0.001 probability level.
† Variances within columns followed by different letters are significantly different at P = 0.05.
‡ NS = not significant.

the sativa × falcata hybrids runs counter to generally accepted theory (e.g., Allard and Bradshaw, 1964). For entry × location and entry × year variances, the lower yielding FFC had greater variances than SSC (Table 6). Lower yields are often associated with reduced entry × environment variances (Lin et al., 1986); however, the opposite was observed in this study. Thus, elite sativa germplasm, which has undergone generations of selective breeding, appears to have greater environmental stability than wild falcata germplasm as well as higher biomass yield. Unfortunately, the intersubspecific sativa × falcata hybrids did not take on the characteristic of the superior elite sativa parentage, maintaining greater instability in most years.

Breeding Implications

This study uncovered potential weaknesses of sativa × falcata hybrid cultivars developed with current falcata germplasm. Although the elite sativa germplasm could carry the weaker falcata germplasm in hybrid combinations for persistence, the biomass yield and biomass heterosis declined as the stand aged. Several genotypes, however, maintained increased heterotic performance through the fourth post-establishment year. The results of this study suggest that selection within falcata breeding nurseries needs to take persistence and longer range yield performance into account, insuring falcata performance through the third and fourth post-establishment years. Potential falcata breeding material also needs to be tested in multiple environments to ensure acceptable performance. Furthermore, selection for increasing biomass yield levels in falcata germplasm should increase the likelihood that transgressive or high parent heterosis would be observed given that mid-subspecies heterosis was in the 10 to 20% range throughout much of the study.

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